QUERCUS × INTROGRESSA, A NEW HYBRID OAK

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A previously undescribed hybrid which is believed to have involved three taxa in the genus *Quercus* L. is reported here from western Missouri. The taxa are: *Quercus muehlenbergii* Engelm., the chinquapin oak, *Q. prinoides* Willd., the dwarf chinquapin oak and *Q. bicolor* Willd., the swamp white oak. The hybrids are putatively the result of matings between introgressants of the two chinquapins (*Q. muehlenbergii* × *prinoides*) and *Q. bicolor.* While such matings in the published accounts of hybridization in *Quercus* have been suggested (Tucker, 1961, & Hardin, 1975), they have been infrequently noted and merit description. The name *Quercus* × *introgressa* was selected to emphasize the fact that one of the parental taxa is, in turn, of hybrid origin.

Quercus × introgressa Thomson, hybrida nova

Arbores 12–20 m altae trunco 47.7 ad 84.9 cm. diametro cortice cinereo fissili ramis patentibus. Ramuli hornotini laeves glabri vel pilis stellatis adspersis praediti. Gemmae apicales hiemales 3–5 ovatae usque rotundatae squamis ovatis 3–5. Folia obovata usque fere linearia, 6.7–15.5 cm. longi, 4.9–6.9 cm. lata, modice stellato-pilosa basi late vel anguste cuneata apice late acuta lobis 2–7 sinu 0.8–1.0 cm. profundo. Petioli 1.3–1.6 cm. longi. Glandes rotundatae vel ovoideae, 1.6–2.0 cm. longae, 1.2–1.6 cm. latae cupulis hemisphaericis pubescentibus squamis ovatis acutis pericarpio cupulam dimidio superante. Pedunculi 2.2–6.6 cm. longi, glabri.

TYPE: **United States:** MISSOURI: ca. 1 km. northeast of Concordia in a pasture adjacent to a rest area along Interstate 70, *P. Thomson 74–161* (Holotype, SIU; Isotype, MO).

Quercus × *introgressa* is known only from Lafayette County, Missouri, where there is a population of thirteen plants. Individuals of both parental taxa, three of *Q. muehlenbergii* × *prinoides,* and one of *Q. bicolor* are present on the site with the putative hybrids. The seventeen plants are situated in a cow pasture, midway on the northeast-facing slope of a low hill just above a small creek. I first observed them from an adjacent rest area along Interstate 70, approximately one kilometer northeast of Concordia, Missouri. It

would seem appropriate, therefore, that an individual of the taxon be colloquially referred to as a Concordia Oak.

Quercus × *introgressa* is most readily distinguished by its long peduncles which bear small, rounded fruit and by its short, narrow leaves. The hybrids are tree-sized plants ranging in height from 12–20 meters and in diameter (measured at breast height) from 47.7 to 84.9 centimeters. Although members of the population were found to be fertile, seedlings and saplings of both these and the parental taxa were not observed in the pastured area. However, the branches of one of the hybrids did extend from the fenced pasture into the rest area. Below these branches, in an area inaccessible to mowing, were several seedlings showing a resemblance to the hybrid tree. Collections were not made of the seedlings. The lack of smaller plants in the pasture is presumably due to what the owner described as heavy grazing by cattle and hogs on the site for many years (personal interview, 1974).

What is striking about the population is the presence of features among eight of the individuals that have values less than the same features in either typical *Quercus muehlenbergii* or *Q. bicolor.* It is believed that the source of this extreme variation in *Q.* × *introgressa* has been hybridization between *Q. muehlenbergii* introgressed by *Q. prinoides* and *Q. bicolor.* Figure 1 shows representative leaves from individuals of the taxa and the putative hybrids.

MATERIALS AND METHODS

Specimens of *Quercus muehlenbergii* Engelm. and *Q. prinoides* Willd. were selected and examined from populations occurring in western Missouri as well as in the herbaria of the Missouri Botanical Garden and Southern Illinois University at Carbondale. The putative hybrids are represented only from collections at the Concordia site and *Q. bicolor* only from herbarium material.

Data supporting hybridization are presented according to the methods of Anderson (1949) and involve only morphological features of the leaves and fruits. Characters used in this study include: lamina length, lamina width at the widest point, number of lobes, petiole length, peduncle length, nut length, nut diameter, and angle of the lamina base.

Three leafy twigs bearing acorns were removed from each field member. Leaf features were measured to the nearest millimeter

Figure 1. Leaf samples from *Quercus muehlenbergii* (lower left), *Q. prinoides* (lower right), an introgressant between them (lower center), *Q. bicolor* (top) and two hybrids (center).

for the terminal leaf of each twig and averaged to represent the individual. Number of lobes per leaf, excluding the terminal lobe, was determined by counting all those occurring between the base and the apex on the right side from the adaxial surface. Numbers were rounded off to the nearest lobe. Angle of the lamina base was determined by attaching a dissecting pin to a 15 centimeter plastic ruler at the zero mark and at right angles to it. Measurements were made by placing the tip of the pin at the junction of petiole and lamina and the shank along the margin of the base. The point at which the ruler crossed the midrib was recorded and divided by the length of the pin. The obtained value yielded the tangent of the angle formed by midrib and margin at the base. Because a ten centimeter pin was impractical for measuring smaller leaves, a five centimeter pin was used for the triangle's base and the value on the ruler was doubled to produce the tangent. Tangent values were converted to degrees from trigonometric tables. Values obtained for the three leaves were averaged and rounded off to the nearest degree. Fruit characters of the individuals were measured and averaged in a manner similar to that for leaf dimensions.

Measurements obtained from herbarium material do not represent averages for individuals, but a sufficient number of specimens was examined to gain an impression of the range of variation for the selected characters for the taxa. Values obtained from the population samples and the herbarium specimens were used to construct a hybrid index and pictorialized scatter diagrams.

The following six characters were employed in constructing the hybrid index: lamina width/length ratio, petiole length, angle of the lamina base, nut length, nut diameter and peduncle length. The numbers 0, 1 and 2 were assigned to represent character values of *Quercus bicolor,* intermediates and *Q. muehlenbergii* × *prinoides* respectively. A hybrid index value for individuals of the population was produced by summing the number of characters occurring in each category according to its assigned value. Thus, an individual of *Q. bicolor* on this index would receive an index value of 0, intermediates a score of 6 and those of *Q. muehlenbergii* × *prinoides* scores of 12. Character values utilized in constructing the hybrid index are presented in Table 1. The character number of lobes was not used in constructing the hybrid index, but was useful in distinguishing *Q. muehlenbergii* and *Q. prinoides.*

Table 1.

Principal morphological features and their values used in distinguishing Quercus bicolor and Q. muehlenbergii X prinoides.

Character	*Q. bicolor*	*Q. muehlenbergii* × *prinoides*
Lamina width/length ratio	0.57–0.90	0.20–0.45
Petiole length	3.0–1.2 cm.	1.7–3.0 cm.
Peduncle length	3.0–8.0 cm.	0.0–2.0 cm.
Angle of the lamina base	11°–17°	25°–45°
Nut length	2.0–3.5 cm.	1.0–1.5 cm.
Nut diameter	1.5–2.0 cm.	0.75–1.2 cm.

RESULTS

Investigation of the site confirmed suspicion of the hybrid parentage because the suspected hybrids and associated oak species on the site are quite well isolated from other oak populations. There is a small grove of post oaks (*Quercus stellata* Wang.) about 400 meters to the northwest, but they are presumably out of effective pollination range (Hardin, 1975). Many of the suspected hybrids possessed peduncles as long as 3.0 cm. or longer, and it is logical to suspect the swamp white oak as one parent as this feature is considered diagnostic for the species (MacKenzie, 1902; Deam, 1940; Steyermark, 1963). The chinquapin oak was a likely candidate for the other parent because of its presence on the site and because several of the hybrid acorns conformed in shape and dimensions to those of that species.

In order to determine whether the observed variation may have been a consequence of hybridization, the plants were compared with the suspected parents by constructing scatter diagrams using values obtained from their morphological features. Comparisons were made with values obtained from herbarium material for *Quercus bicolor* and *Q. muehlenbergii,* and the characters of lamina length, lamina width, nut length and nut diameter for several of the hybrids had values for one or more of these which were less

than the same characters of either suspected parental taxon. Hybrid character values surpassing the lower limit of variation for both *Q. bicolor* and *Q. muehlenbergii* were considered extreme. The limits used to distinguish typical from extreme variation were those of the species having the lowest value for a character. Thus, for nut length *Q. bicolor* varies from 2.0 cm. to 3.0 cm. and *Q. muehlenbergii* from 1.5 cm. to 2.0 cm. Variation among the hybrids was considered to be extreme for any individual having acorns less than 1.5 cm. in length. Of the eight individuals having extreme character values, five possess only one feature, two individuals display two features and one demonstrates smaller values for all four characters. Table 2 summarizes the occurrence of extreme variation for the eight members.

For two years prior to and following the discovery of the hybrid site, the two chinquapin species have been the subject of extensive examination in western Missouri. Population sampling has yielded quantitative data in support of a morphological characterization

Table 2.

Occurrence of extreme character values among eight members of the hybrid population.

	Lamina		Nut	
Specimen Number	length < 11.0 cm.	width < 5.0 cm.	length < 1.5 cm.	diameter < 1.2 cm.
74–150	X			
74–152	X			
74–153	X	X	X	X
74–154		X	X	
74–156		X		
74–157	X			
74–161	X		X	
74–166	X			

based on an examination of 15 populations (6 of the shrub and 9 of the tree) and 331 specimens collected from them. More recently the study has expanded to include populations in Illinois, Iowa, Nebraska, Kansas, Oklahoma, Texas and New Mexico. Although there seems to be much hybridization and introgression between them, typical members of each taxon may be distinguished on the basis of growth habit, length and width of the lamina, length and diameter of the acorn and number of lobes on one side of the lamina (Table 3). Populations of *Quercus muehlenbergii* in western Missouri differ most clearly in leaf features which vary continuously from typical *Q. prinoides* to typical *Q. muehlenbergii* with respect to length but are narrower. Leaves vary from 6.0 cm. to 18.0 cm. in length but from 2.5 cm. to 7.0 cm. in width. By comparison, typical *Q. muehlenbergii* ranges from 12.0 cm. to 20.0 cm. in length and 5.0 cm. to 9.0 cm. in width. *Quercus prinoides* varies from 4.0–10.0 cm. in length and 2.0–5.0 cm. in width. "Typical" means the leaves conform to descriptions provided by the authors of the taxa and determinations of herbarium specimens by competent botanists.

Figure 2 depicts lamina length and width values from a representative population of *Quercus muehlenbergii* occurring approximately 40 kilometers to the west of the hybrid location in adjacent Jackson County, Missouri. The same attributes scored from her-

Table 3.

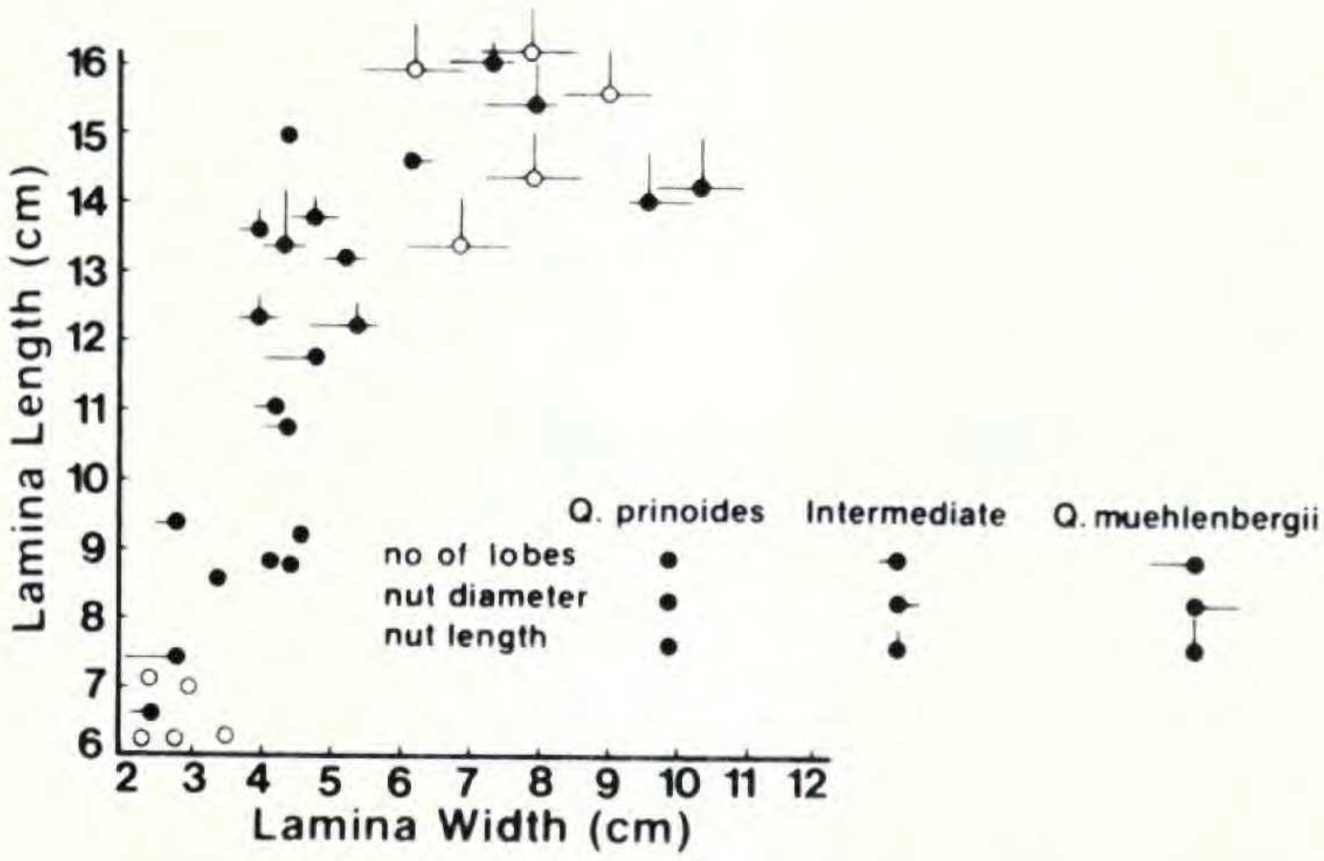
Principal morphological features and their values used in distinguishing Quercus muehlenbergii and Q. prinoides.

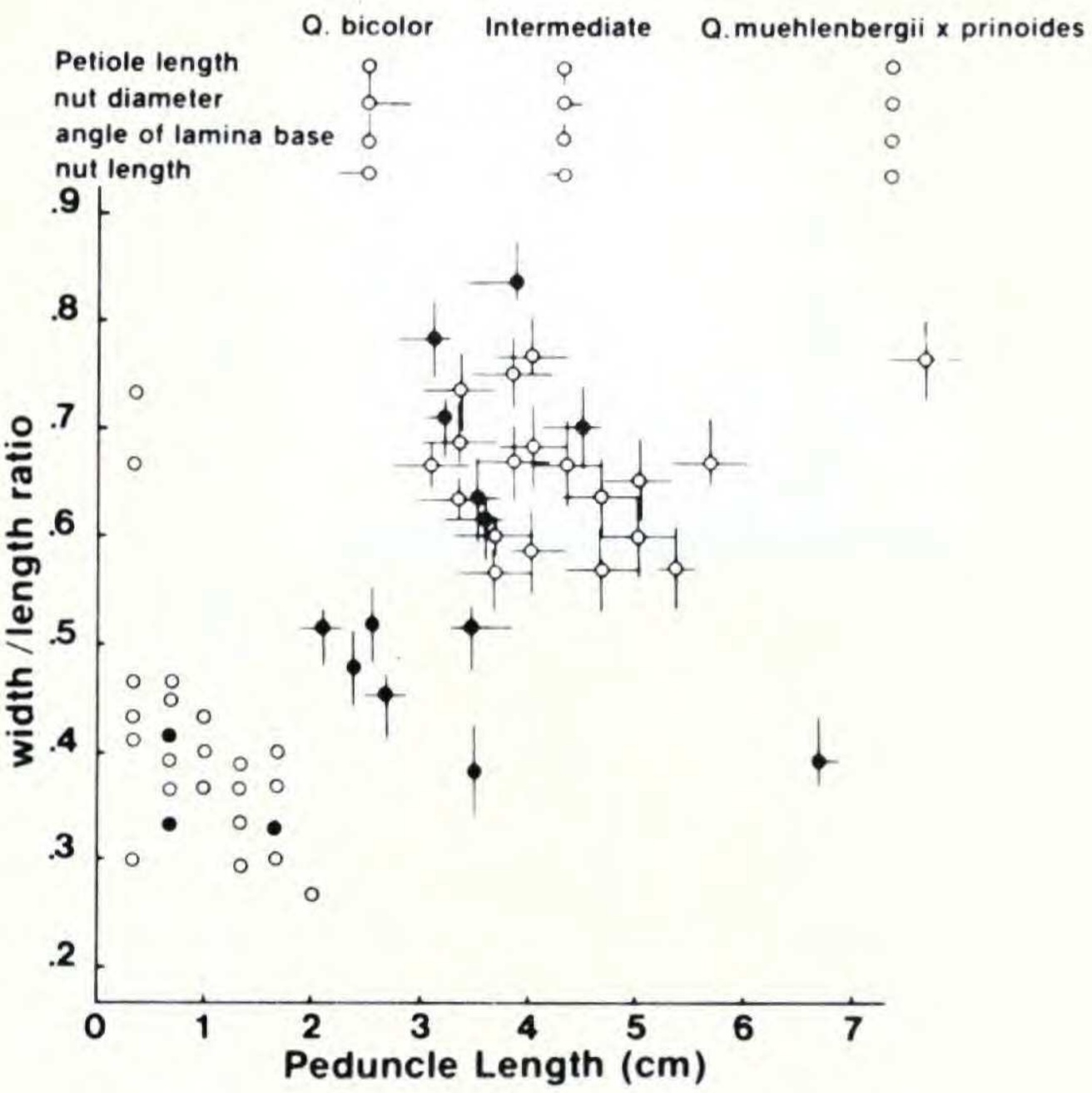
Character	Q. muehlenbergii	Q. prinoides
Lamina length	12.0–20.0 cm.	4.0–10.0 cm.
Lamina width	5.0–9.0 cm.	2.0–5.0 cm.
Number of lobes	9–12	3–7
Nut length	1.5–2.0 cm.	0.5–1.4 cm.
Nut diameter	1.2–1.8 cm.	0.5–1.0 cm.
Growth habit	medium to large tree	shrub or small tree

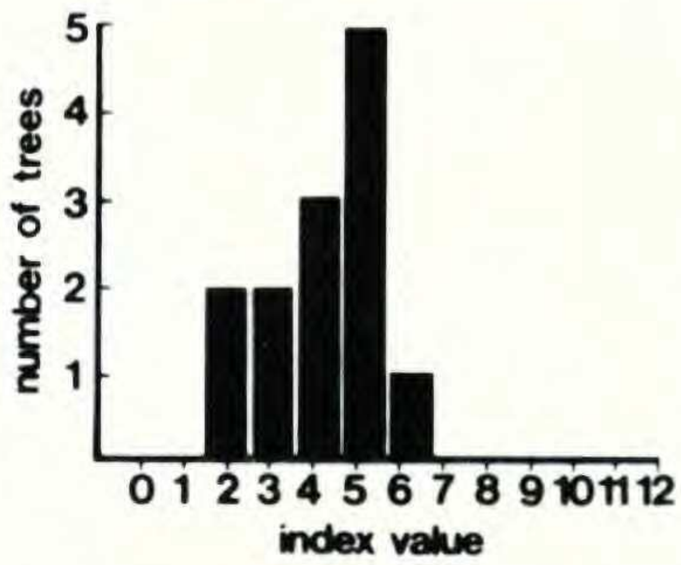
barium material of a few individuals of *Q. prinoides* and *Q. muehlenbergii* have been added as open circles. The characters have been pictorialized to include number of lobes, nut length and nut diameter. Thus five characters are represented for each individual. Plants of the population are all tree-sized individuals but the graphic pattern seems to suggest an influence by the shrub. Leaves vary in length from typical *Q. prinoides* to typical *Q. muehlenbergii,* but the majority are less than 6.0 cm. in width. Nut length varies in a manner similar to lamina length, but nut diameter conforms more to *Q. prinoides* values. Number of lobes is mainly less than 9, again a feature more typical of the shrub. The features tend to co-vary but not absolutely, a pattern suggestive of plants displaying introgressive hybridization as described by Anderson (1949).

While the variation present in chinquapin oak populations is not the subject of this paper, it may bear directly upon the observation of extreme character variation in the hybrid population. At the site three narrow-leaved individuals of *Quercus muehlenbergii* are present together with the putative hybrids and occupy a position near the top of the slope above them. Consequently, pictorialized scatter diagrams were prepared using values from the Jackson County population of *Q. muehlenbergii* introgressed by *Q. prinoides.* Because of the wide range of variation in leaf dimensions ratios were used for those features rather than their absolute values. Thus, when leaf shape, expressed as a width/length ratio, is compared to peduncle length for introgressed *Q. muehlenbergii* and *Q. bicolor,* distinction of the hybrids is more readily observable (Figure 3). The three individuals of *Q. muehlenbergii* × *prinoides* from the hybrid site were scored and are included as solid circles among the members of the population. The remaining closed circles of Figure 3 represent the members of the hybrid population.

Seven of the hybrids appear intermediate between *Quercus muehlenbergii* × *prinoides* with respect to leaf shape and peduncle length, and six conform more to values for the swamp white oak. Included as metroglyphs in Figure 3 are the characters of petiole length, nut diameter, angle of the leaf base and nut length. For the first of these, two of the hybrids have intermediate values, ten *Q. bicolor* values and one *Q. muehlenbergii* × *prinoides* value. Five of the hybrids have acorns conforming to *Q. muehlenbergii* × *prinoides* in width, seven are intermediate and one has acorns more typical of *Q. bicolor.* For the feature of nut length, four are like







Figures 2–4. 2 (top), analysis of variation for *Quercus muehlenbergii* introgressed by *Q. prinoides;* 3 (center), analysis of variation of *Q.* × *introgressa;* 4 (bottom), hybrid index for the hybrid population.

Q. bicolor, five are intermediate, and four have *Q. muehlenbergii* × *prinoides* values. Five hybrids have intermediate lamina base angles while eight are like *Q. bicolor.* The analysis of variation presented here would seem to support interpretation of the population as one of hybrid origin. However, the occurrence of characters as described above would suggest that the population members are not all first generation hybrids. Individuals intermediate in the scatter diagram have hybrid index values of 6, 5, 5, 5, 5, 5 and 4 while the remaining six have values of 4, 4, 3, 3, 2 and 2. Hybrid index values for the population are presented graphically in Figure 4.

DISCUSSION

The hybridization described here differs from other cases described in *Quercus* in the past inasmuch as three taxa are believed to be involved. Participation of a third taxon (*Quercus prinoides*) has resulted in production of individuals with variations for some characters which exceed those of the parents. Although the nature of that variation is recognizable here as diminutive features among the hybrids, this certainly would not always be the result of an influence by a third species. Of course, other explanations may be offered for the occurrence of excessively large or small features. Tucker (1970), in discussing extreme character variation in hybrid populations of *Q. gambelii* and *Q. havardii,* concluded that transgressive segregation was more likely responsible for small leaf size than the influence of a third species (*Q. turbinella*) because the hybrids exceeded all three taxa in another characteristic, foliar pubescence. This factor does not seem to apply in *Q.* × *introgressa,* as none of the extreme character values exceed typical *Q. prinoides.* It is more probable that genetic combinations which have led to diminutive variation in some of the hybrids have come to them via hybridization with tree-sized chinquapins introgressed by the dwarf.

A peripheral question concerns the status of the two chinquapin oaks. Their existence as distinct species has been called into question in recent years by Steyermark (1957, 1963), Gleason and Cronquist (1963), Stephens (1973), Hardin (1975) and historically by others (Britton, 1886; Farwell, 1923; Camp, 1934). Extensive studies of both taxa by Steyermark during preparation of the *Flora of Missouri* (1963) led him to discount the coexistence of the taxa at the specific level as his inspection found them to be varying con-

tinuously in many characters across a wide range of habitats where the two are sympatric. Therefore, he recognized a single species, *Quercus prinoides* Willd. and followed Gleason's treatment (1952) in separating the former species at the varietal level, i.e., *Q. prinoides* Willd. as *Q. prinoides* var. *prinoides* and *Q. muehlenbergii* Engelm. as *Q. prinoides* var. *acuminata* (Michx.) Gl. Steyermark (1957) further separated the latter variety into narrow and broad leaved forms, forma *acuminata* and forma *alexanderi.*

In contrast, Stephens (1973) in his *Woody Plants of the North Central Plains* maintains the taxa as distinct species but describes their intergradation on intermediate sites. He states, "The species are seen to intergrade along slopes of hills in eastern Kansas with *Quercus muehlenbergii* occupying the upper slopes, *Q. prinoides* the lower slopes and intermediates on the mid-slopes." Fernald (1970), in *Gray's Manual of Botany* also separates the plants at the specific level.

Although it is not the purpose of this report to support either of the interpretations summarized above, a nomenclatural point should be made that *Quercus* × *introgressa* is equivalent to *Q. prinoides* var. *acuminata* × *Q. bicolor* if *Q. muehlenbergii* is considered a variety. This too is undescribed.

As to the status of *Quercus* × *introgressa,* it would seem to be a mixture of F_1 and/or F_2 hybrids and backcrosses to *Q. bicolor.* The term hybrid swarm would be appropriate.

Finally, the following key is offered as a guide to the recognition of the taxa important to this study.

KEY TO QUERCUS × INTROGRESSA AND RELATED TAXA

1. Peduncles exceeding the petioles in length by twice or more. . . . . 2.
   2. Leaves twice as long as wide, fruit small (1.5 cm. × 1.0 cm.) and longer than wide. . . . . *Q.* × *introgressa.*
   2. Leaves less than twice as long as wide, fruit larger (2.5 cm. long × 1.5 cm. wide). . . . . *Q. bicolor.*

1. Peduncles up to but not exceeding the petioles in length. . . . . 3.
   3. Trees with leaves 6.0–18.0 cm. in length and 4.0–9.0 cm. wide or wider with 6–11 shallow lobes on a side each containing one principal vein and terminating in a mucronate tip. . . . . 4.
      4. Leaves 1½–2 times longer than broad with 6–10 lobes. . . . . *Q. muehlenbergii* × *prinoides.*
      4. Leaves less than 1½ times as long as broad, lobes 9–12. . . *Q. muehlenbergii.*
   3. Shrubs with leaves 4.0–8.0 cm. in length, 2.5–5.0 cm. in width, lobes 3–7. . . . . *Q. prinoides.*

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LITERATURE CITED

ANDERSON, E. 1949. Introgressive hybridization. 109 pp. Hafner. New York.

BRITTON, N. L. 1886. Notes on *Quercus muehlenbergii* Engelm. Bull. Torrey Bot. Club **13:** 41.

CAMP, W. H. 1934. Notes on certain Ohio oaks. Ohio Jour. Sci. **34:** 422.

DEAM, C. C. 1940. Flora of Indiana. Dept. of Conservation. Indianapolis, Indiana.

FARWELL, O. A. 1923. Notes on the Michigan flora. Papers Michigan Acad. Sci. Arts and Letters. **3:** 93.

FERNALD, M. L. 1950. Gray's manual of botany. 8th ed. American Book Company. New York. (Corrected printing 1970, D. Van Nostrand Co.)

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. 3 vols. Hafner Publishing Co. New York.

_____, & A. CRONQUIST. 1963. Manual of vascular plants of Northeastern United States and adjacent Canada. D. Van Nostrand Co. Princeton, New Jersey.

HARDIN, J. W. 1975. Hybridization and introgression in *Quercus alba.* Jour. Arnold Arb. **56:** 336–363.

MACKENZIE, K. K. 1902. Manual of the flora of Jackson County, Missouri. 242 pp. Press of the New Era Co. Lancaster, Penn.

PERSONAL INTERVIEW. 1974. MR. WALTER LUETJANS, owner of study site. Concordia, Missouri.

STEPHENS, H. A. 1973. Woody plants of the North Central Plains. Univ. of Kansas Press.

STEYERMARK, J. A. 1957. New combinations and forms in the Missouri flora. Rhodora **62:** 130.

_____. 1963. Flora of Missouri. Iowa State Univ. Press.

TUCKER, J. M 1961. Studies in the *Quercus undulata* complex. I. A preliminary statement. Am. Jour. Bot. **48:** 202–208.

_____. 1970. Studies in the *Quercus undulata* complex. IV. The contribution of *Quercus havardii. Ibid.* **57:** 71–84.

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